Revue suisse de Zoologie 106 (4): 1013-1024; décembre 1999

The identity of *Glomeris quadrifasciata* C. L. Koch (Diplopoda: Glomeridae)

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The identity of *Glomeris quadrifasciata* C. L. Koch (Diplopoda: Glomeridae). - The synonymy of *Glomeris quadrifasciata* C. L. Koch, 1847, with *G. undulata* C. L. Koch, 1844, recognized by Verhoeff (1931), is confirmed. *Glomeris oblongoguttata* Verhoeff, 1894, stat. n. is the valid name for *Glomeris quadrifasciata* sensu Verhoeff (1911) from South Tyrol. This taxon is classified as a species closely related to *G. transalpina* C. L. Koch, 1836, by Verhoeff (1911). Allozyme electrophoretic data agree with morphological results. Possible glacial refugia and postglacial colonization, which might explain the actual distribution of *G. oblongoguttata* and *G. transalpina*, are discussed. Specific separation of both taxa is concluded to have happened before the Pleistocene (> 1.6 mio years BP).

Key-words: Diplopoda - *Glomeris* - revision - allozymes - postglacial colonization - refugia.

INTRODUCTION

In most diplopods, the gonopods as highly differentiated sclerotized structures have successfully been used for species separation and distinction. *Glomeris*, however, do not have gonopods. The telopods with their syncoxite that are used for copulation (Haacker 1969) show only minor differences among species and even show variation within some species (e.g. Verhoeff 1932, 1936a and Schubart 1934, *G. undulata* nominate form and f. *conspersa*). In addition, they have never been tested for their qualification as isolating mechanism. Molecular data instead, might be more useful for taxonomic studies in these animals. In fact, allozyme electrophoretic data have recently been successfully used to analyse whether the *Glomeris*-taxa *hexasticha* and *intermedia* are species or subspecies (Hoess *et al.* 1997). Taxonomic studies and revisions in *Glomeris* are complicated by the fact that no type material was indicated in the *Glomeris* literature until the mid of the 20th century. In any case, however, type material cannot be used in allozyme studies because it is usually preserved in ethanol that destroys enzyme activity. We therefore collected new material in the areas of the taxa concerned and we depend for identification on morphological characters, such as

Manuscript accepted 11.05.1999

the colour pattern, the grooves on the shield and the shape of the last tergite, that are usually sufficiently outlined in the original descriptions.

For our allozyme-based genetic analysis of the Central European *Glomeris* species, we also sampled a population of *Glomeris quadrifasciata* sensu VERHOEFF (1911) (nec Koch, 1847). We found that the oldest available name for Verhoeff's taxon is *G. oblongoguttata* which was first described as a local variety of *G. transalpina* (VERHOEFF 1894) and later classified as a variety of his *G. quadrifasciata* (VERHOEFF 1911). VERHOEFF (1911) considered his taxon as closely related to *G. transalpina*. This relationship is here confirmed by allozyme data. Furthermore, based on this allozyme data set, we postulate glacial refugia for and postglacial colonization of *G. oblongoguttata* and *G. transalpina*.

MATERIAL AND METHODS

One population sample of *G. oblongoguttata* (endemic for South Tyrol and the Bergamo Pre-Alps) and eight population samples of *G. transalpina* from large parts of its range were analyzed (number of specimens in brackets): *G. oblongoguttata*: Latsch (17); *G. transalpina*: Pfynwald (19), Simplon (2), Loucherhorn (2), Airolo (13), Brugnasco (16), Albula (11), Lago di Poschiavo (2), Glurns (19). The small samples have been included especially in order to analyse ways of postglacial colonization, they are problematical as population samples for electrophoretic studies, however. The main colour characters which separate *G. oblongoguttata* and *G. transalpina* are shown in Fig. 1, and the distribution of both taxa (compiled from literature) and the localities of the sample sites are given in Fig. 2.

We used routine enzyme electrophoretic methods of our laboratory (cf. SCHOLL *et al.* 1978). Vertical starch gel electrophoresis was conducted using the same buffer systems as before (HOESS *et al.* 1997). 18 enzyme loci were analyzed. The enzymes investigated and the loci scored (in brackets) are: aspartate aminotransferase (Aat-1, Aat-2), glyceraldehyd-3-phosphate dehydrogenase (Gapdh), glucose-6-phosphate isomerase (Gpi), hexokinase (Hk), leucine aminopeptidase (Lap), L-lactate dehydrogenase (Ldh-1, Ldh-2), malate dehydrogenase (Mdh-1, Mdh-2), malic enzyme (Me), mannose-6-phosphate isomerase (Mpi), peptidase (Pep), 6-phosphogluconate dehydrogenase (Pgd6), phosphoglucomutase (Pgm), superoxide dismutase (Sod-1, Sod-2) and sorbitol dehydrogenase (Sodh).

The zymograms were photographed (Polaroid) for reference. We refer to observed electromorphs as alleles which are identified by their electrophoretic mobility (in mm) relative to previously studied species (HOESS *et al.* 1997). We used the BIOSYS-1 programme package (SWOFFORD & SELANDER 1989) for calculation of allele frequencies and data treatment. Using the matrix of Nei's distance (NEI 1978), a phenogram of the populations was created by average linkage cluster analysis (UPGMA).

With the allozyme data, we also tried to test the biological species concept by MAYR & ASHLOCK (1991) where species are defined as groups of interbreeding natural populations that are reproductively isolated from other such groups. For the usability of small samples cf. GORMAN & RENZI (1979).

Heterozygosity was not estimated and tested with Hardy-Weinberg-expectations because most samples were collected in a very small sampling area. *Glomeris* have low individual mobilities. This increases the chance of picking up siblings. The assumptions that underly the Hardy-Weinberg-principle are therefore not given for these samples.

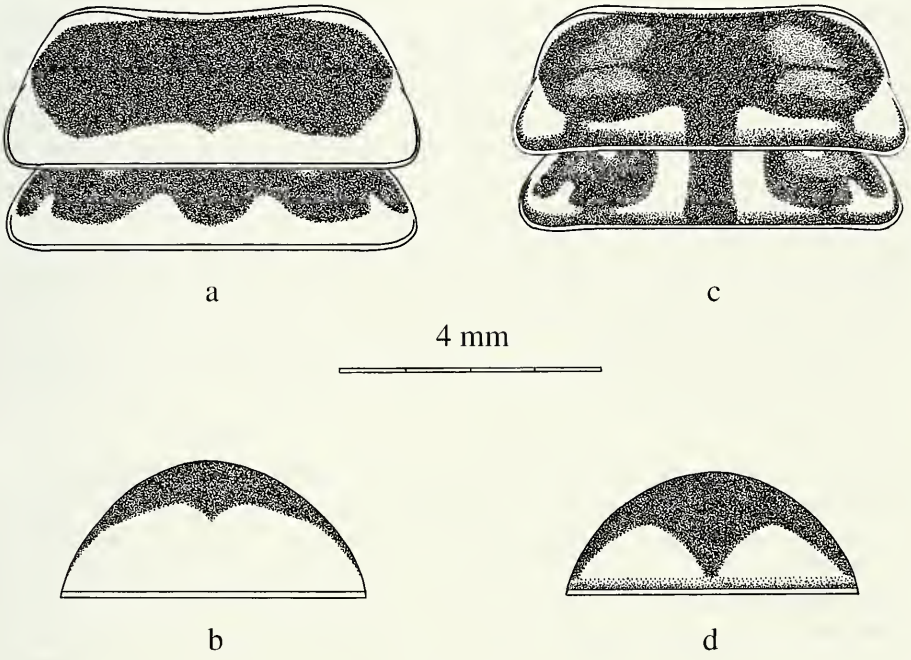

FIG. 1

Colour patterns of *Glomeris transalpina* (a, b) and *G. oblongoguttata* (c, d). Shield (2nd) and 3rd tergite (a, c) (dorsal view) and last (12th) tergite (b, d) (posterior view) (females). Scale: 4 mm.

TAXONOMY

Glomeris oblongoguttata Verhoeff, 1894 stat. n. Figs 1 c, d; 2

Glomeris transalpina C. L. Koch var. *oblongoguttata* Verhoeff, 1894: 17, Sulden (South Tyrol); VERHOEFF 1902: 180.

Glomeris transalpina C. L. Koch var. *spinalemontis* Verhoeff, 1902: 180, Mt. Spinale (South Tyrol); VERHOEFF 1906: 220.

Glomeris quadrifasciata C. L. Koch sensu VERHOEFF 1911: 113-114, 139 (nec Koch, 1847); ATTEMS 1927: 255; VERHOEFF 1929: 563; VERHOEFF 1930: 655; VERHOEFF 1931: 429, 433, pl. 7, figs 33, 34 [part]; VERHOEFF 1932: 641; VERHOEFF 1936a: 430; VERHOEFF 1936b: 231; VERHOEFF 1937: 168; STRASSER & MINELLI 1984: 197; FODDAI *et al.* 1995: 12.

Glomeris quadrifasciata sensu VERHOEFF (loc. cit.) (nec Koch, 1847) var. *sevini* Verhoeff, 1931: 431, Bergamo Pre-Alps; VERHOEFF 1937: 167.

Glomeris quadrifasciata sensu VERHOEFF (loc. cit.) (nec Koch, 1847) var. *brixiensis* Verhoeff, 1931: 432, Brescia (Lombardia).

Diagnosis: Shield with broad yellow-red margins at the outer parts of front and hind edge. Central dark spots on tergites 2-11 parallel-sided or divergent posteriorly. Dark spot on the last tergite triangular, almost reaching the hind edge with the tip. No principal groove but 3-7 accessory grooves on the shield. Last tergite in the male with a notch in the hind margin. Dark pigment always in well defined spots. Speckles often present.

VERHOEFF (1911) designated, with modified and additional characters, *G. quadrifasciata* as a species closely related to *G. transalpina* Koch. *G. quadrifasciata* sensu Verhoeff differs from *G. quadrifasciata* Koch by the following characters: the former has a large, triangular, dark spot on the last tergite that hardly separates the two yellow-red spots, and the shield has a broad yellow-red margin at the outer parts of the hind edge, too (Fig. 1). These characters do not lie within the range of variation of *G. undulata* Koch (see below) to which Koch's *G. quadrifasciata* belongs. This implies that Verhoeff's taxon is a different species. Verhoeff's use of the name *G. quadrifasciata* C. L. Koch is therefore incorrect. VERHOEFF (1931) actually recognized this fact but he did not explicitely rename his taxon.

Glomeris transalpina var. *oblongoguttata* Verhoeff, 1894, is the oldest available name for Verhoeff's taxon.

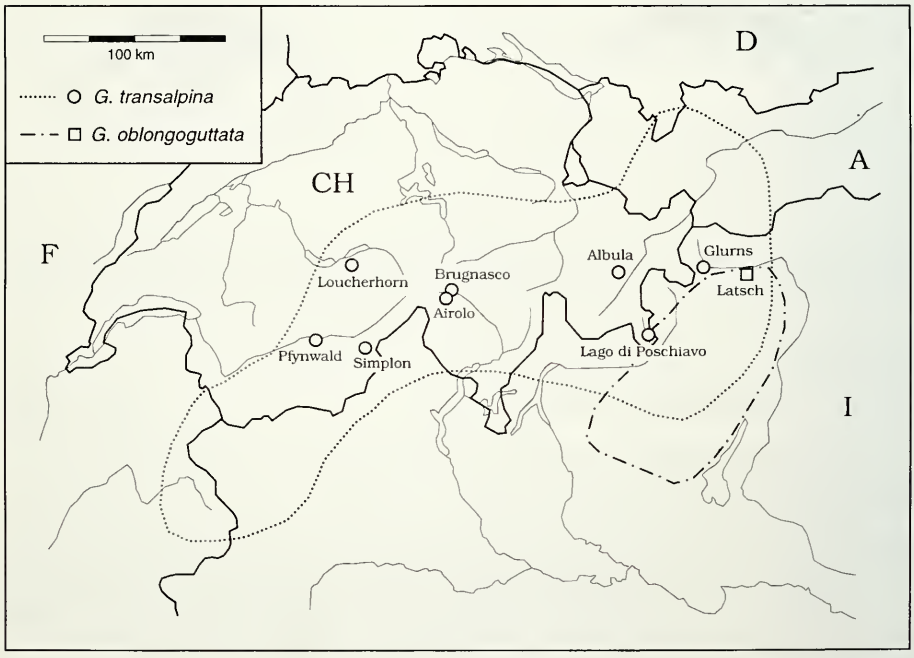

FIG. 2

Distribution (compiled from literature) and sample sites of *Glomeris transalpina* and *G. oblongoguttata*.

Glomeris undulata C. L. Koch, 1844

The synonymy of *G. undulata* presented here is restricted to the names that are needed within the scope of this paper:

Glomeris undulata C. L. Koch, 1844: H. 40, pl. 8, South Germany.

Glomeris conspersa C. L. Koch, 1847: 89, South Germany [synonymized with *G. undulata* by Hoess & Scholl 1999: 657, 659].

Glomeris quadrifasciata C. L. Koch, 1847: 91, origin unknown, probably South Germany; C. L. Koch 1863: 108, pl. 49, figs. 98 a, b, c, one specimen indicated from the museum at Bamberg; Verhoeff 1931: 433 [part].

Glomeris tridentina Latzel, 1884: 118, South Tyrol [synonymized with *quadrifasciata* by Verhoeff 1902: 177].

Glomeris conspersa quadrifasciata C. L. Koch sensu Verhoeff 1902: 180; Verhoeff 1906: 166, 177.

Diagnosis: Shield with broad yellow to red margins only at the outer parts of the front edge. Central dark spots on tergites 2-12 variable: parallel-sided or divergent posteriorly in the nominate form, convergent posteriorly in f. *conspersa*. No principal groove, except some specimens of f. *conspersa* from the South-eastern Alps which have one, but with 3-4 accessory grooves on the shield. Only some males of nominate form with a notch in the hind margin of the last tergite. Dark pigment next to the central spots usually scattered in speckles, seldom without speckles.

Koch described (1847, 1863) and illustrated (1863) *Glomeris quadrifasciata*. On the shield, this taxon shows no complete groove (character 1), but it has a broad yellow band (character 2) along the front edge. The last tergite has two large yellow-red spots that are separated by a broad dark band (character 3) which widens towards the front edge. The middle segments show four bands (character 4) of yellow-red spots that are separated in the middle by a dark band made of parallel-sided spots (character 5). Characters 1, 2, 3 and 5 are typical for what is presently recognized as *G. undulata* Koch, whereas character 4 lies within the range of variability of *G. undulata* which is known to be one of the most variable species of the genus. Typically, *G. undulata* shows speckles which are absent in *G. quadrifasciata*. However, there are some varieties of *G. undulata*, that do not express the speckles (see e.g. Verhoeff 1931; confirmed by own data from electrophoretically analyzed specimens). Consequently, *G. quadrifasciata* does not provide any character for its own. We therefore agree with Verhoeff (1931) who recognized *G. quadrifasciata* Koch as a synonym of *G. undulata* Koch.

Latzel (1884) synonymized *G. quadrifasciata* Koch with *G. connexa* Koch. This is not acceptable because the significant characters 1 and 2 are different in *G. connexa* (see also Verhoeff 1902).

Verhoeff (1902) first classified *quadrifasciata* as a subspecies of *G. conspersa*; but characters 3, 4 and 5 are different in the latter.

Glomeris transalpina C. L. Koch, 1836 Figs 1a, b; 2; 4

This species shall also be diagnosed here. It was classified as closest related to *G. oblongoguttata* by Verhoeff (1911) which we confirm by allozyme data later in this paper.

TABLE 1

Allele frequencies of the 14 polymorphic loci for all populations of *Glomeris oblongoguttata* (Latsch) and *G. transalpina* (other populations). Number of examined specimens in brackets. A = average number of alleles per locus over all 18 loci.

Locus/ Allele	Population								
	Latsch	Glurns	Lago di Poschiavo	Albula	Brugnasco	Airolo	Loucher-horn	Simplon	Pfynwald
	(17)	(19)	(2)	(11)	(16)	(13)	(2)	(2)	(19)
Aat-1									
105	0.53	0.55	0.25	0.22	0.43	0.69	0.75	1	0.32
104	0.06	-	-	-	-	-	-	-	-
100	-	-	-	0.11	-	-	-	-	-
97	0.38	0.45	0.75	0.67	0.57	0.31	0.25	-	0.68
76	0.03	-	-	-	-	-	-	-	-
Gapdh									
111	-	0.08	-	-	-	-	-	-	-
109	1	0.92	1	1	1	1	1	1	1
Gpi									
100	1	1	1	1	1	1	1	1	0.92
96	-	-	-	-	-	-	-	-	0.08
Hk									
103	0.74	0.39	0.25	0.25	0.12	0.50	0.75	0.75	0.21
100	0.26	0.61	0.75	0.75	0.88	0.50	0.25	0.25	0.79
Ldh-2									
100	0.68	-	-	-	-	-	-	-	-
97	0.23	-	-	-	-	-	-	-	-
93	0.09	-	-	-	-	-	-	-	-
82	-	1	1	1	1	1	1	1	1
Mdh-1									
105	-	-	-	-	0.28	0.37	-	0.50	0.63
100	1	1	1	1	0.72	0.63	1	0.50	0.37
Mdh-2									
102	-	-	0.75	-	-	-	-	-	-
100	0.66	0.82	0.25	0.80	0.88	0.88	0.50	1	0.94
99	0.09	-	-	-	-	0.06	-	-	-
98	0.09	0.06	-	0.20	0.04	-	0.50	-	-
97	0.04	0.03	-	-	0.04	-	-	-	-
95	0.04	0.06	-	-	-	0.06	-	-	0.03
94	0.04	-	-	-	-	-	-	-	-
91	0.04	0.03	-	-	0.04	-	-	-	0.03
Me									
102	-	0.94	1	1	0.09	0.25	-	-	-
100	1	0.06	-	-	0.82	0.56	-	1	1
98	-	-	-	-	0.09	0.19	1	-	-
Mpi									
104	0.18	1	1	1	1	1	0.75	1	1
100	0.41	-	-	-	-	-	-	-	-
97	-	-	-	-	-	-	0.25	-	-
95	0.09	-	-	-	-	-	-	-	-
91	0.32	-	-	-	-	-	-	-	-

Pep									
104	0.29	-	-	-	-	-	-	-	-
102	0.18	-	-	0.05	0.14	0.27	-	-	-
100	0.53	0.10	-	0.18	0.80	0.61	1	0.50	0.74
98	-	0.40	1	-	0.03	0.04	-	-	0.05
96	-	0.50	-	0.77	0.03	0.08	-	0.50	0.21
Pgd6									
106	-	-	-	-	0.10	0.14	1	-	-
104	0.06	-	-	-	-	-	-	-	-
100	0.94	1	1	1	0.90	0.86	-	1	1
Pgm									
100	-	0.14	-	0.05	0.11	0.35	0.50	-	0.61
97	-	0.86	1	0.95	0.89	0.65	0.50	1	0.39
95	0.05	-	-	-	-	-	-	-	-
93	0.50	-	-	-	-	-	-	-	-
89	0.45	-	-	-	-	-	-	-	-
Sod-2									
100	0.77	0.40	0.50	0.41	0.47	0.46	-	-	0.45
98	-	0.05	0.25	0.36	0.28	0.31	0.75	0.50	0.08
95	0.23	0.29	-	0.05	0.06	0.23	0.25	0.50	0.31
93	-	0.26	0.25	0.18	0.19	-	-	-	0.16
Sodh									
112	-	0.11	-	0.21	0.87	0.62	1	-	0.47
109	0.03	0.52	0.50	-	-	-	-	-	0.03
106	-	0.26	0.50	0.79	0.13	0.38	-	1	0.29
103	-	0.11	-	-	-	-	-	-	0.21
100	0.97	-	-	-	-	-	-	-	-
A	2.22	1.94	1.33	1.61	1.94	1.83	1.33	1.22	1.78
	Val Venosta		Grisons		Ticino		Bernese Alps	Valais	

Diagnosis: Shield with broad (yellow-)red margins at the outer parts of the front and hind edge. Central dark spots of tergites 2-11 confluent with the remaining dark pigment, convergent posteriorly but not reaching the hind edge. Dark spost on the last tergite triangular but ending far away from the hind edge. No principal groove but 3-4 accessory grooves on the shield. Never a notch in the hind margin of the last tergite. Dark pigment always in well defined spots. Speckles rarely present.

RESULTS

The alleles observed and their frequencies are listed in Table 1 except for the four loci Aat-2, Lap, Ldh-1 and Sod-1 that were monomorphic, and all populations of both taxa were fixed for the same alleles, viz. Aat-2^{100}, Lap^{100}, Ldh-1^{100} and Sod-1^{99}, respectively. Three other loci were monomorphic except for one or two populations, and the same allele was found in both taxa: Locus Gapdh, allele $Gapdh^{109}$ (except the *G. transalpina* population from Glurns with one additional allele), locus Gpi, allele Gpi^{100} (except the *G. transalpina* population from Pfynwald with one additional allele),

and locus Mpi, allele Mpi^{104} (except the *G. transalpina* population from Loucherhorn with one additional allele and the *G. oblongoguttata* population with three additional alleles). Locus Ldh-2 was monomorphic in all populations of *G. transalpina* (allele Ldh-2^{82}), the *G. oblongoguttata* population, however, had three alleles that were not observed in *G. transalpina*. The other loci showed high genetic polymorphism. Excluding the populations with small sample sizes (N < 10), the average number of alleles per locus (total: 18 loci) was 2.22 in *G. oblongoguttata* and 1.61-1.94 in the *G. transalpina* populations.

G. oblogoguttata and *G. transalpina* were clearly genetically distinct by alternative alleles at the loci Ldh-2 and Pgm (Table 1). Additionally, the two geographically closest populations of each taxon namely Latsch and Glurns (distance about 25 km, both localities are in the same valley) showed remarkable differences in the allele frequencies at five other loci. These loci were Hk, Me, Mpi, Pep and Sodh (Table 1).

Of the 59 alleles recorded at the 18 loci, 21 alleles were found in both taxa, 15 alleles were only observed in *G. oblongoguttata*, and 18 alleles were only observed in *G. transalpina*, 13 of these 18 alleles of *G. transalpina* were widespread in the range of that species.

Several alleles of *G. transalpina* were restricted in their distribution to certain regions (Table 1). At locus Mdh-1, the allele Mdh-1^{105} was only found in Ticino (populations Brugnasco and Airolo) and Valais (populations Simplon and Pfynwald). At locus Me, the allele Me^{102} was fixed or nearly fixed in the three eastern populations (Glurns, Lago di Poschiavo and Albula), it was rare in Ticino and was not present in the three western populations (Loucherhorn, Simplon and Pfynwald). This allele is substituted by alleles Me^{100} and Me^{98} in the western populations. At locus Pgd6, the allele Pgd6^{106} was only found in the Ticino populations (Brugnasco and Airolo) and in Loucherhorn.

TABLE 2

Nei-distances D in pairwise comparisons of populations of *Glomeris transalpina* and *G. oblongoguttata* (sample sizes > 10).

		G. transalpina				
		Pfynwald	Airolo	Brugnasco	Albula	Glurns
G. transalpina	Airolo	.037				
	Brugnasco	.038	.020			
	Albula	.158	.098	.120		
	Glurns	.149	.086	.121	.034	
G. oblongoguttata	Latsch	.264	.238	.268	.375	.324

Table 2 shows the genetic distances D (Nei 1978) in pairwise comparisons of all populations (sample sizes > 10) using all 18 loci. These distances varied from 0.02 - 0.16 among different populations of *G. transalpina* and from 0.24 - 0.38 among populations of the two taxa.

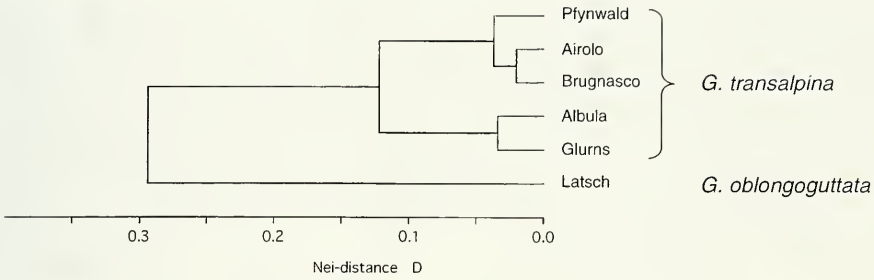

FIG. 3

UPGMA dendrogram using Nei's coefficient of genetic distance for populations of *Glomeris transalpina* and *G. oblongoguttata* (sample sizes > 10).

The Nei distances were graphically transformed into an UPGMA dendrogram (Fig. 3). *G. oblongoguttata* is separated from *G. transalpina* at a distance level of 0.29. The *G. transalpina* populations are found in two subclusters that separate at a distance level of D = 0.12 and contain the Valais and Ticino populations on the one hand and the eastern populations on the other hand.

DISCUSSION

The most distant populations of *G. transalpina*, Glurns and Pfynwald, that are about 225 km apart, share at least one allele at each locus. On the other hand, the closest populations of both taxa (*G. transalpina* population from Glurns and *G. oblongoguttata* population from Latsch) that are found only 25 km apart in the same valley have alternative alleles at two loci (Ldh-2 and Pgm). This indicates that the two taxa belong to different gene pools. This is also supported by five other loci where the allele frequencies between the Latsch and Glurns populations are very different (Hk, Me, Mpi, Pep and Sodh). Specimens with transition in morphological characters that would indicate hybridisation are not known. We therefore conclude that *G. transalpina* and *G. oblongoguttata* are in fact different species. However, these species are closely related. In a previous study (HOESS *et al.* 1997) we found that *G. undulata* (sub *G. conspersa*), which shares characters 1 and 2 (see above) with *G. transalpina*, is genetically more distant to *G. transalpina* than *G. oblongoguttata*.

The locally observed alleles, the allele substitution observed at the Me locus, and the Nei-D values that are graphically interpreted in the dendrogram show two subgroups within *G. transalpina*, an eastern subgroup from Grison and its adjacent valleys, and a western subgroup from Ticino to Valais and the Bernese Alps, respectively. However, there is no reason to assume that these subgroups are specifically distinct. The subgroups are not correlated with the variation of the colour pattern. Instead, each population has some own trends in altering the basic colour pattern. It is therefore not appropriate to rank the subgroups as subspecies.

FIG. 4

Supposed glacial refugia and ways of postglacial colonization of *Glomeris transalpina* (see text for explanation).

The geographically restricted alleles suggest that there must have been at least two glacial refugia for *G. transalpina* from where colonization of the presently inhabited localities has started (Fig. 4). The eastern subgroup with Albula, Glurns and Lago di Poschiavo probably had a refuge in the mountains north of Bergamo and/or Brescia. Lago di Poschiavo may have been colonized from the Bergamo refuge through the Adda Valley, while Glurns was colonized from the Brescia refuge. The origin of the Albula population is not clear, the allozyme data are not conclusive in this case. All western populations may originate from the nunataks in Ticino. The Valais most probably was colonized only once over the Nufenen, and the Bernese Alps independently from that over the Nufenen and the Grimsel. The alleles that are restricted to Valais and Ticino do not favour a separate colonization of the Simplon from the south. Loucherhorn was a Nunatak and might have been inhabited by *G. transalpina* during the Pleistocene. The allozyme data, however, show that this population is very close to the Valais and Ticino populations which suggests that Louchernhorn was colonized from the south.

Taking into consideration its present distribution, we assume that *G. oblongoguttata* had its glacial refuge on both sides of the Oglio Glacier like the eastern populations of *G. transalpina*. This, of course, requires genetic isolation during the Pleistocene. We, therefore, conclude that specific separation of *G. oblongoguttata* and *G. transalpina* occurred before the Pleistocene (> 1.6 mio years BP).

At present, both species inhabit woods of the mountainous, subalpine and the adjacent levels. *G. transalpina* prefers higher regions compared to *G. oblongoguttata*. Thus, especially in the pre-alps, colonization would not be confined to the valleys. This renders the interpretation of postglacial colonization more difficult, but shows that mountain chains are not necessarily a barrier for dispersal. The limited present ranges of both species, as compared to e.g. the widespread *G. marginata*, may be due to the crooked topography of the Alps. The scarcity of records of *G. transalpina* in the Northern Alps also supports the hypothesis of southern refugia and a northward expansion.

ACKNOWLEDGEMENTS

M. E. Braunwalder, B. Gantenbein, P. Marmet and P. Sonderegger helped us gather the glomerids used in this study. L. Beer, L. Frauchiger and V. Siegfried assisted in the laboratory work. H. Baur gave nomenclatorial advice.

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